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I.

The Electric Discharge of the Electric Eel, *Electrophorus electricus* (Linnaeus).

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(Plates I & II; Text-figures 1-6).

INTRODUCTION.

The electrical power developed by certain fishes has stirred the imagination of investigators since the earliest times, but an adequate, thorough, explanation of the phenomenon is still unavailable. Since there is still much to be explained in the physiology of skin and muscle, from which the electric organs of the various electric fishes are derived, we thought it well to attempt an explanation of the external manifestation by an analysis of the electrical currents and potentials as they may be examined at present and, perhaps, to suggest the internal electrical mechanism from this analysis. The present paper then, is largely concerned with the physics of the external electrical phenomena.

Of all the electric fishes the Electric Eel is the largest and develops most power, and to our minds offers the most suitable medium for investigation. Besides, the other electric fishes, Torpedo (*Raia*), *Malopterurus*, the Electric Mormyridae, and *Astroscopus*, are not so easily available to us as the eel, and do not withstand the necessary laboratory manipulation as well.

The Electric Eel is more or less circular in cross-section, depressed at the head and compressed at the tail. The length is roughly ten times the greatest diameter.

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Dr. Max Mapes Ellis (1913) describes the position of the electric organs of the fish rather fully and since the position is of some importance in the following discussion we think it advisable to quote him.

"There are three pairs of electric organs in *E. electricus*, the large electric organs, the secondary organs or the organs of Hunter, and the bundles of Sachs. The large organs and the organs of Hunter both begin a short distance behind the viscera and run nearly the whole length of the fish. The bundles of Sachs are found only in the posterior half of the fish. The large organ of each side is more or less quadrant shaped in cross-section, and is of greatest diameter about a centimeter back of its origin. It tapers gradually back of this point becoming more nearly circular in cross-section until it disappears a few centimeters from the end of the tail. It lies on each side of the haemal spine above the anal fin musculature and below the muscle *ventralis*. In the region of its maximum size the top of each organ is on a level with the vertebral centra, but as the caudal end is approached, the dorsal portion of each organ lies more and more ventrad.

"The organ of Sachs consists of a series of bundles of fibers which resemble both muscle and electric tissue. From the middle of the body to the caudal end of the large electric organs, the organs of Sachs lie on a *dorso-lateral* surface of the latter, just below the muscle *ventralis*. The bundles of this organ wrap around the large electrical organ obliquely in a latero-ventral direction. They extend further ventrad as the caudal extremities of the large organ are neared. They finally close over the ends of these. The organs of Sachs increase in diameter caudad.

"The organs of Hunter are triangular in cross-section and much smaller than either of the other two pairs of organs. They are in the anal fin region and lie between the muscles *pinnalis analis externalis* and the muscles *pinnalis analis internalis*. Dorsally they are separated from the large organ by the remnants of the muscles *lateralis imus*. They taper off as their caudal ends are approached and terminate a few centimeters in front of the ends of the large organs."

Dr. Ellis reproduces plates, not included here, and continues with a description of the organs:

"Both the large organs and the organs of Hunter are composed of plates of tissue which run parallel to the large axis of the fish. In the large organs these plates are more or less arched ventrally in cross-section. In the small organs they are almost flat. The number of these plates seem to be rather constant in each organ, regardless of the size of the fish. Bois-Raymond (1881) (in Sachs, Zitteraal, p. 32) gives the following table:

Observer	Body length	Plates in Large Organ	Plates in Small Organ
Sachs	31 cm.	30	14-19
Knox	48.5	32	17
Pahlberg	68.5	32	13
Hunter	71	35	15
Kupffer and Keferstein.....	120	31	Not given
Humboldt	Not given	36	20
Sachs	Not given	30	14-19

"According to Sachs, who confirmed in general the work of Pacini, the large electric organs are made up of minute units about .14 mm. broad, which lie at right angles to the long axis of the plates. Each unit is divided near the center by a vertical partition. On the anterior face of this are several papillae which do not reach the wall of the unit. On the posterior face are fewer papillae which reach out to the wall of the unit. Between the latter are several minute papillae. It is on this side that each receives its nerve-fibers."

We see no reason to change these descriptions.

The Electric Eel is a sluggish fish, given to lying still in shallow water for long periods which are broken only to move to the surface of the water to gulp air, a process which is repeated at intervals of about four minutes. We have found these fish will drown if denied access to air for as little as fifteen minutes, a significant fact, perhaps, which might indicate a high oxidation rate, especially when discharging electricity.

The fish is reported from the fresh waters of northern South America, ranging from the Amazon Basin northward to the Orinoco Basin.

The first scientific reports of the electricity of the Electric Eel appear to be those of Richer, published 1729, and since then there are several hundred titles in the bibliography. For the sake of convenience we do not list the complete bibliography but suggest that reference to Dean's (1916-1923) *Bibliography of Fishes* be made.

However, it might be as well to discuss briefly some of the earlier findings, which, despite the crudity of the measuring apparatus available at the time, seem to us to be highly suggestive. We do not quite see, in view of many of these reports, how subsequent investigators, with still crude apparatus but apparatus which was a decided improvement over the original, should have become as confused as they apparently did, and it seems strange that with the improvement in electrical measuring instruments through the years the research into the nature of the discharge should have diminished considerably.

The first detailed evidence that the discharge was one of "electric fluid" seems to have been adduced by Williamson in 1775, who reports that he received an electrical shock through his finger when it was inserted in a stream of water flowing from a tank in which an Electric Eel had been disturbed. He further reports that a person insulated by standing on glass bottles could receive a shock by placing his hands in the water containing an eel. This report followed by two years the evidence that the Torpedo could give an electric shock, adduced by Walsh (1774) in letters to Benjamin Franklin.

Garden (1775), writing from America at the same period, offers some proof that the discharge was electrical and further, his description suggests that some of the five eels he saw were suffering from cataracts of the eye, a condition we find in most of our larger eels and which we suspect is due to the continual electric discharges. If this is so it is, apparently, the only self-inflicted effect of the electricity we have found to date.

It is at once apparent from most of this early literature that the eels available to the investigators were in poor condition; no doubt some of them were dying, a condition which might have had its advantages since the early investigators estimated the strength of the discharge by the sensation felt in the joints of the fingers, the hands, wrists, elbows, etc., following the methods of Cavendish's work on the Torpedo.

However, Schönbein (1841) reports seeing a fish in London in 1841 which had lived there for more than a year. This fish seemed to be quite healthy and gave an unexpectedly heavy shock which made a chain of people holding hands, the extreme left and right hands being placed in the water, leap into the air. This shock was repeated in rapid succession and he concluded that the eel could either divide its electricity or renew it at will. As against most previous investigators, Schönbein was able to report a spark across a small air-gap. He suggested that the nerve of the organ is an important, or perhaps the most important, part of the organ since if this is severed there is no more electricity. Matteucci (1844, 1847), on the contrary, thought that the nerves had little to do with it since he was able to dissect out part of the electric tissue and keep it for as long as eight days in an electrically active state. Humboldt (1806), however, had stated that until more was known of the general function of nerve it was useless to attempt further work. He compares the shock to that of a

Voltaic Pile and comments on the utter lack of effect on an electrometer. Lethely in 1843 endeavored to show that the electricity was derived from the brain and spinal cord and that the nervous and electrical forces were the same.

Faraday (1839, 1844) made a number of remarkably accurate observations on the Electric Eel—remarkable in their accuracy and in that his opportunities for observing the fish were extremely limited both because of the scarcity of specimens and because they were not his own and his use of them was limited by his unwillingness to risk damaging them by experiments. (Incidentally there cannot have been many eels available anywhere at that time and the cost of those that were available comparatively high. Garden (1775) mentions fifty guineas as the price of the smallest of five ranging in size from two to about four feet which were presented for sale in Charleston about 1775. The price could not have been much, if anything, less in England, and the chance of obtaining them there much slimmer.) However, in spite of meager facilities, meager apparatus, and obviously sick fish, Faraday was able to determine that the current flowed from the head to the tail of the fish externally, that the largest shock was obtained from a point close behind the body proper and near the end of the tail. Our points of maximum potential correspond closely to this. Faraday also noted that the current must be of "low intensity but of great quantity," that the fish must be conscious of its own capabilities, and that the eel would quit discharging when it discovered that the electricity had no effect on the irritant. All these observations but the last, of which we have but *a priori* knowledge, fit nicely into the present calculations.

Pacini, 1853, postulated that the internal current of the electric organs must flow from the nutritive to the electrical surfaces of the cells, and since the nutritive surface is always posterior to the electric, the current must flow from tail to head.

Throughout this paper positions of electrodes and lengths of bodies of the eels measured are given in centimeters although they were actually measured in inches. The factor used in conversion is 2.5 cm. per inch instead of 2.54 cm. per inch. This is for convenience, on the one hand, and because the use of the more accurate figure would imply an exactitude of position impossible with such an animal. The total error involved by use of the conversion factor 2.5 is a little over one centimeter for the largest eel, negligible because it was not always possible to control the position of the animal during a series of discharges and observations to within one centimeter.

Our method of preparing the Electric Eel for taking the electrical readings is to remove it from the water, allow it to dry for a few minutes on a dry, insulated surface, and then put it into the measuring trough where it will usually lie quietly for as long as one hour, although we found it expedient to return the fish to the water at shorter periods. Heavy rubber gloves are worn when touching the eel, for the discharge may be dangerous, even with an exhausted eel which may have its voltage reduced by as much as one-third and which will not discharge as frequently as a fresh one.

DISCUSSION.

Because the electric tissue is modified muscle tissue, it seems reasonable to suppose that the chemical processes by which energy is released in the electric organs are similar to those by which energy is released in muscles, but whereas in muscles most of the energy made available by the chemical transformations is released as mechanical work and only a minute fraction is released as electrical energy, in the electric organs this ratio is reversed and a large part of the energy is used to produce an electric discharge. On this supposition, the principal consequence of the modifica-

tion of muscle tissue into electric tissue would be to provide an organization of the cells in an electric network to make possible a discharge in cascade, so combining the cellular electromotive forces as to produce voltages more than a thousand times greater than those developed in ordinary muscular activity.

It does not seem necessarily true that the action of electric tissue is more complex than that of muscle tissue. On the contrary, there is reason to expect that it will be more easily understood. For it seems reasonable to suppose that muscular activity is a conversion of energy in two stages, first from the chemical form to the electrical, then from the electrical form to the mechanical. If this be true, then the action of electric tissue may show the isolated first stage of muscular action, and study of the transformation of energy in electric organs may be important for understanding the initial phase of muscular activity.

Since the skin of the eel and the tissue surrounding the electric organs are electrically conducting, it is possible to study the discharge by connecting the terminals of a suitable measuring instrument to wires in contact with the skin. When potential differences are measured without drawing appreciable current, as was the case in most of our observations, they are found only between points on the skin which include between them some longitudinal segment of one of the electric organs. (The points of contact with the skin must not both be anterior nor both be posterior to the discharging organ, and they must not both be on a common circumference of the eel.) If the points of contact are far enough apart to include between them the whole lengths of the electric organs, no appreciable change is made in the observed voltages by having them still farther apart.

When no appreciable current is drawn, that is, when the eel is on "open circuit" except for the leakage of current through its own tissue, an anterior point on its skin is always during the discharge electrically positive with respect to a posterior portion, which is in accordance with Pacini's rule.

When considerable current is drawn, the potential distribution over the skin of the eel is naturally modified by the flow of current in the neighborhood of the electrodes. In one of the few experiments we made in which considerable currents were drawn, an odd effect was noticed. The eel being out of the water and in contact with certain wires which offered a highly conducting path between anterior and posterior parts, it was gently prodded to make it discharge. After about five minutes of intermittent discharge, the skin over the posterior, electrically negative parts was observed to be bleached, where it touched the wires, to a shade much lighter than that elsewhere on the body. The eel was then returned to the water. After some ten or fifteen minutes similar sharply defined bleached areas were observed where the skin over the anterior parts had formerly touched the wires. With these connections the current density may have attained instantaneous values of the order of 0.1 ampere per cm.² of skin, as may be inferred from the area in contact and certain observations (to be described later in this paper) made to determine the power of the discharge. Although such a current density must be much greater than any produced when the eel discharges under water and the current flows through its whole skin, the eel, nevertheless, showed no effects of the discharge beside the bleaching, and the bleached areas soon returned to the normal color.

Eilenfeld, using a string galvanometer of short period, has measured the peak voltages obtained between the extremities of a number of electric eels. He has reported the existence of two distinct peak voltages developed by any one eel. Observations previously reported¹ by two of the present

¹ Coates, C. W., and Cox, R. T. Preliminary Note on the Nature of the Electrical Discharges of the Electric Eel, *Electrophorus electricus* (Linnaeus). *Zoologica*, New York, 1936, Vol. 21, No. 11, pp. 125-128.

authors have confirmed this. We have not observed voltages as high as some of those reported by Eilenfeld. From observations under various conditions on a number of eels, we conclude that the maximum voltage by no means increases proportionately with the length of the eel. A potential difference of nearly 200 volts was developed by an eel 29 cm. long, but no voltages greater than about 300 volts have been found with larger eels, though observations have been made out of water on open circuit on eels ranging in length to about a meter and in water on eels as long as 240 cm.

The cathode-ray oscillograph, by reason of its almost instantaneous response to an applied voltage, is especially suited to observations of electric discharges in tissue. Its essential part is a vacuum tube in which a well defined beam of electrons, accelerated by a potential difference of several hundred volts, passes between flat electrodes to strike a fluorescent screen. The electrodes are commonly in the form of rectangular plates. A pair of such plates being fixed one on either side of the beam with their surfaces parallel to it, a difference of potential established between them will cause a deflection of the electron beam approximately proportional to the applied voltage. If the voltage is applied suddenly, the luminous spot in which the electron beam strikes the fluorescent screen will move rapidly across the screen, and the persistence of the fluorescence and of the visual sensation will give the appearance of a luminous streak. This trace can be photographed with a lens sufficiently rapid. We have used an F2 and an F3.5 lens with Eastman Super X film.

Commonly, the tube is equipped with two pairs of deflecting plates, mutually at right angles, to which voltages can be applied at the same time. A usual practice is to connect a "sweep circuit" to the horizontally deflecting pair of plates. This circuit generates a voltage which increases uniformly in time to a certain value and then returns very rapidly to zero. Under the action of this voltage, the luminous spot moves horizontally across the fluorescent screen at a nearly uniform rate for a certain distance and then returns almost instantaneously to its starting point. A transient voltage under investigation being applied at the same time to the vertically deflecting plates, the luminous spot has at any instant a horizontal displacement proportional to the time and a vertical displacement proportional to the instantaneous value of the transient voltage. The trace on the fluorescent screen is thus a graph showing the variation in time of the transient voltage. The scales both of voltage and of time can be fixed by the use of a standard alternating voltage.

We have found convenient for this research the Radio Corporation of America Cathode Ray Oscillograph Type TMV-122-B, an instrument developed for general laboratory utility. It contains in the same case with the oscillograph tube a number of accessory circuits, including a sweep circuit of variable frequency, circuits with amplifier tubes through which the voltages applied to the deflecting plates can be either amplified or attenuated, and circuits for converting power at 110 volts and 60 cycles to the types required in the oscillograph.

Since the potential differences developed by the eel are longitudinal, measurements are conveniently made by removing the eel from the water and laying it in a trough of insulating material ribbed with transverse wires evenly spaced. The skin of the eel is kept in contact with these wires. By means of dial switches, any wire can be connected to any one of the deflecting plates of the oscillograph.

Most of the observations to be described here were made on two eels. Eel I was 92 cm. in length. Its girth was 21 cm. at a distance of 20 cm. from the snout and the same at a distance of 50 cm. from the snout. Eel II was 88 cm. long and had a girth of 18 cm. at a distance of 20 cm. from the snout and a girth of 16.5 cm. at a distance of 50 cm. from the snout.

In discussing most of these observations, the eel, or, rather, any one of its electric organs, can be regarded as some sort of power line, with all the significant variations occurring in one dimension only, that of the length of the eel. The quantity most directly measured with the oscillograph is the potential difference between two points on this line. But potential is not the quantity in terms of which the discharge is most conveniently described. For example, consider a point on the eel's tail, posterior to all the electric organs. The potential of such a point with respect to the eel's head varies in the discharge from zero to a peak negative value and back to zero, though no electromotive force is developed nearer this point than the end of the nearest electric organ. It is more convenient to describe the discharge in terms of some quantity of which the value at any point is wholly determined by the transformations of energy in the immediate neighborhood of that point. Such a quantity is the potential gradient or voltage per unit length along the eel. In the discharge of an electric organ, if no appreciable current is drawn, the potential gradient remains practically zero at any point anterior or posterior to the organ, while it rises to a maximum and falls again to zero at any point along the electric organ. If at any instant the potential gradient is uniform over the distance between two given points, the potential difference between them at this instant is simply the product of the potential gradient by the distance. More generally, the potential difference between two points is the integral from one point to the other of the potential gradient.

One of the first questions to present itself is whether the potential gradient varies synchronously at all points along the discharging electric organ, so that the potential gradient at any given point maintains during the discharge a fixed ratio to the potential gradient at every other point, or whether on the contrary there is a time lag in the rise and fall of the potential gradient between one point and another. This question is easily decided by the oscillograph. One plate of each pair in the oscillograph tube is connected to a point somewhere near the middle of the electric organ. The other plate of the horizontally deflecting pair is connected near the anterior end of the electric organ and the other plate of the vertically deflecting pair is connected near the posterior end. The organ is thus divided into an anterior and a posterior segment in such a way that the potential difference over the anterior segment produces a horizontal deflection of the luminous spot on the fluorescent screen of the oscillograph and the potential difference over the posterior segment produces a vertical deflection. If the potential gradient varies synchronously at all points, then the potential difference over the anterior segment will maintain a constant ratio to the potential difference over the posterior segment. The horizontal deflection will therefore be in a constant ratio to the vertical deflection, and the oscillographic trace will be a straight line. If, on the contrary, there is a time lag between the variations of potential gradient at different points along the electric organ, then the path traced by the luminous spot will have a changing slope as the ratio of the potential differences over the two segments changes, and the trace will be a loop of some kind.

In Pl. I, Figs. 1 and 2, are shown oscillographic traces photographed during the discharge of Eel II when the horizontally deflecting plates were joined to the extremities of an anterior segment between points at 15 and 35 cm. from the snout and the vertically deflecting plates were joined to the extremities of a posterior segment between points at 35 and 70 cm. from the snout. The traces of several discharges appear in each picture because the time of exposure was much greater than the time of one discharge. The traces clearly show that the phase of the discharge differs between the anterior and posterior segments. The sense of the difference is, however, not indicated. Since there is nothing to show whether the luminous spot traversed the loop clockwise or counter-clockwise, it is impossible to

tell from the pictures whether the potential difference over the anterior segment leads or lags behind the potential difference over the posterior segment.

Another observation was made to decide this question. The sweep circuit was connected to the horizontally deflecting plates, the timing period being set at 1/60 sec. Two points on the skin of Eel II, 20 and 70 cm. from its snout, were connected to one of the vertically deflecting plates, and two intermediate points, 25 and 50 cm. from the snout, were connected to the other vertically deflecting plate. Thus, there were connected in parallel between the vertically deflecting plates two segments, one extending between the points at 20 and 25 cm. from the snout, the other extending between the points at 50 and 70 cm. from the snout. Since the extreme points of the two segments were connected to one plate and the intermediate points to the other, potential differences in the two segments produced opposing deflections of the luminous spot. The segments were chosen far apart in order to provide the greatest possible time lag. The connections made established two short circuits in the electric organ, but auxiliary observations showed that a short circuit of one part of the electric organ does not drastically change the discharge in another part.

Pl. I, Fig. 3, shows an oscillographic trace photographed with these connections. Because the time of exposure was much greater than the timing period of the sweep circuit, several discharges appear in confused superposition on the right of the picture. But two discharges are shown distinctly on the left. The potential difference developed in the anterior segment caused a deflection downward, that in the posterior segment a deflection upward, and the progression of time was toward the right. Hence, it is evident that the discharge begins in an anterior part and progresses toward the posterior.

✓ From Pl. I, Fig. 1, it is clear that successive discharges are sometimes very different from one another. Traces of the sort shown in this picture were, however, not very frequent. The more regular pattern of Pl. I, Fig. 2, was more often obtained. It appears to be typical of the more intense discharge of the two reported by Eilenfeld. We shall call this the major discharge and certain evidence will be given which makes it probable that this discharge is generated in the large electric organs of the eel.

From inspection of Pl. I, Fig. 2, certain inferences can be made concerning the propagation of the discharge. We have to consider not only the variation in time of the potential gradient at a given point on the electric organ, but also the variation from point to point along the organ of the potential gradient at any given instant. These two variations can be regarded as constituting together a surge or pulse of electric gradient running along the electric organ from anterior to posterior. Ahead of this pulse and behind it the potential gradient is zero. As the front of the pulse advances into any given segment of the electric organ, it builds up potential difference over that segment. As the rear of the pulse progresses out of a given segment, the potential difference over that segment falls. It is convenient for discussion to divide the pulse into three sections, a rising slope, a plateau, and a falling slope. The division is arbitrary and the sections must not be expected to show sharp boundaries. At any instant, the rising slope comprises that segment of the electric organ in which the potential gradient is rising, the plateau comprises the segment in which the potential gradient is changing slowly enough to be regarded as constant, and the falling slope comprises the segment in which the potential gradient is falling. The segment of the organ included in any one section of the pulse is, of course, continuously changing as the pulse progresses down the organ.

In Pl. I, Fig. 2, the lower horizontal side represents the building up of potential difference over the anterior segment of the organ, the segment extending between points at 15 and 35 cm. from the snout. As the rising

slope of the pulse reaches the point at 35 cm., the potential difference starts to rise in the posterior segment, and the trace accordingly starts to bend toward the vertical. When the rising slope has entirely passed the point at 35 cm., the whole anterior segment is occupied by the plateau of the pulse. The potential gradient is no longer changing in any part of the anterior segment and the voltage over this segment is for the time constant. It will be noticed that the lower side of the loop is horizontal for most of its length; the voltage in the posterior segment does not rise appreciably until the voltage in the anterior segment has attained almost its peak value. This means that the rising slope of the pulse is short in comparison with the anterior segment, so that when the rising slope reaches the 35 cm. point, the anterior segment is already largely covered by the plateau.

The nearly vertical right side of the loop shows the voltage rising in the posterior segment while it is maintained practically constant in the anterior segment. The voltage in the anterior segment does not fall appreciably until the voltage in the posterior segment has almost reached its peak, as is shown by the sharp upper right corner of the loop and the horizontal upper side. The plateau of the pulse is thus almost long enough to cover the whole length of both segments, a distance of 55 cm.

The upper side of the loop shows the voltage falling in the anterior segment while it is maintained practically constant in the posterior segment. At the sharp upper right corner, the leading point of the falling slope of the pulse is just entering the anterior segment at 15 cm. from the snout. At the rounded upper left corner, the leading point of the falling slope is just entering the posterior segment at 35 cm. from the snout, having traversed the anterior segment. During this process the voltage in the anterior segment has fallen to a small fraction of its peak. Therefore, most of the falling slope must be comprised in the length of the anterior segment, a distance of 20 cm.

The pulse of potential gradient in the major discharge has thus a short rising slope, probably less than 10 cm. long, a long plateau, about 50 cm. long, and a fairly steep falling slope, not much more than 20 cm. long. The whole pulse would appear to be longer than the large electric organ. This simply means that there is no instant in which the whole pulse is developed in the organ, the front of the pulse running off the posterior end of the organ before the falling slope is entirely developed at the anterior end. These dimensions of the pulse are, of course, very roughly estimated. The form of the pulse appears to vary not only with the size of the eel, but also between eels of approximately the same size. In oscillographic traces obtained with Eel I in the same way as those of Pl. I, Fig. 2, were obtained with Eel II, the loops are much narrower and less rectangular than those shown in Pl. I, Fig. 2.

It should also be made clear that the plateau is a region in which the potential gradient at any given point is constant in time, but not a region in which the potential gradient at a given instant is uniform over all points. If the potential gradient had a uniform value all along the plateau, the peak voltage over any segment of the electric organ shorter than the plateau would be the product of this uniform value by the length of the segment. The peak voltages over two such segments would thus be in the same ratio as the length of the segments. That this is not the case is shown by the shape of the loop in Pl. I, Fig. 2. The peak voltage over the anterior segment, represented by the horizontal distance across the loop, is considerably greater than the peak voltage over the posterior segment, represented by the vertical distance across the loop, although the length of the anterior segment is 20 cm. and the length of the posterior segment is 35 cm.

The loop of Pl. I, Fig. 2, carries, of course, no time calibration and, therefore, gives no indication of the speed at which the pulse travels. But

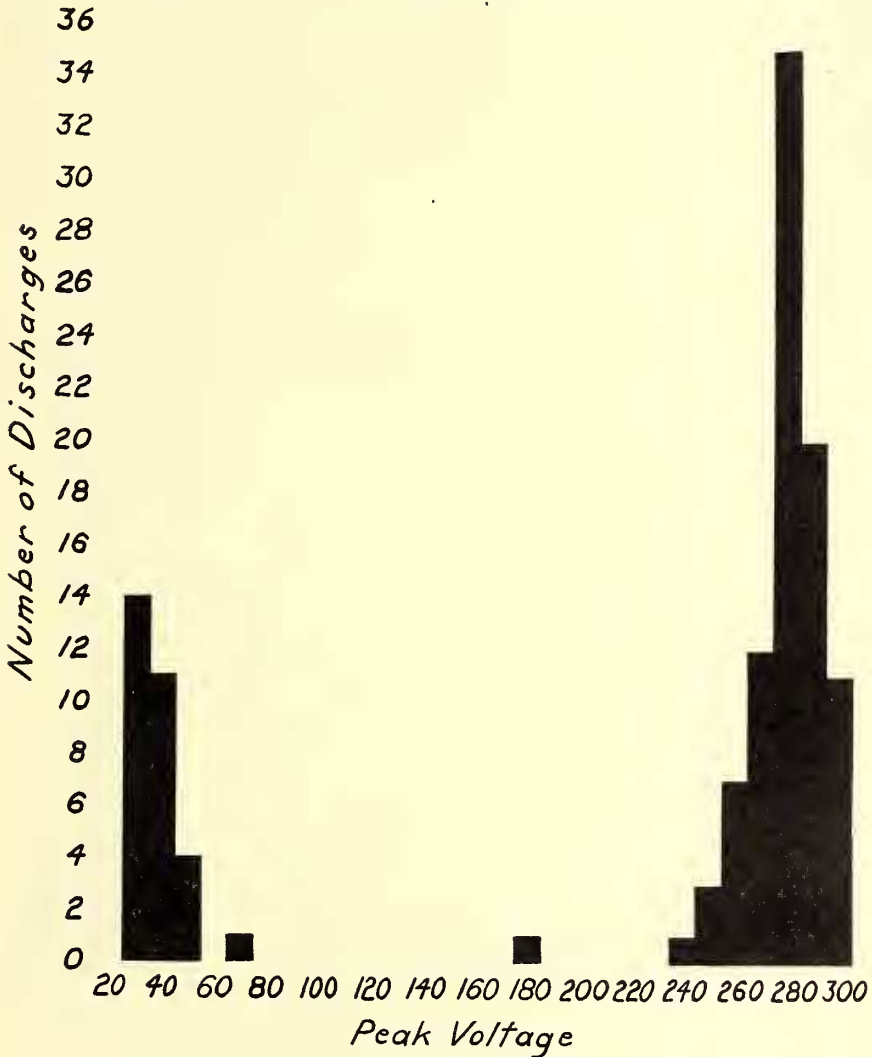
from Pl. I, Fig. 3, in which the heavy base line denotes 1/60 sec., it appears that the whole discharge in both segments takes about .003 sec. This is the time between the instant at which the front of the pulse reaches the point 15 cm. from the snout and the instant at which the rear of the pulse reaches the point 70 cm. from the snout. Hence, it is the time required for the pulse to traverse a distance of 55 cm. in addition to the whole length of the pulse itself, which is perhaps 80 cm. or more. The pulse thus appears to travel about 1.5 meters in .003 sec., and to have a speed therefore of the order of 500 meters per second. Other estimates, to be given later in this paper, show the same order of magnitude.

Several series of observations were made in order to identify more precisely the different types of discharge by their peak voltages as developed between different points along the eel and by the sequence in which they occur after excitation of the eel. The sequence could be studied only by having the timing period of the oscillograph long enough to show a number of discharges during one period. The period chosen was 1/20 sec. The fluorescent screen was photographed with a motion picture camera making 16 exposures per second. The end of the exposure cut off sharply the luminous trace on the fluorescent screen. The end being thus marked, and the time of exposure being less than the timing period of the sweep circuit, the order in time of two or more discharges occurring during one exposure was evident. The beginning of the luminous streak, on the other hand, was gradual because of the afterglow on the fluorescent screen, which carried over to each exposure a faint record of the motion of the luminous spot just preceding the exposure. In the most fortunate of these observations, this afterglow persisted over the whole interval between two successive exposures and so gave a continuous record. In other observations, there was a brief interruption of the record for one or two hundredths of a second between each two successive exposures.

With different connections of the oscillograph to Eel I, the peak voltages of more than 800 discharges were measured to the nearest multiple of 10 volts. Text-fig. 1 shows the distribution with respect to peak voltage observed when one of the deflecting plates of the oscillograph was connected to the snout of the eel and the other was joined to a point 85 cm. from the snout, near the tip of the tail. It is clear that nearly all the discharges observed are grouped around a higher and a lower peak voltage. The discharge of higher peak voltage we have called the major discharge, and that of lower peak voltage we shall call the minor discharge. Besides the discharges which can be classified in one or the other of these types, there appear certain others, in number about 5 per cent. of the total recorded, which could not be so classified. These are especially numerous in one series of observations in which one vertically deflecting plate of the oscillograph was connected to the snout of the eel and the other to a point 55 cm. from the snout. The distribution with respect to peak voltage of the discharges recorded with these connections is shown in Text-fig. 2. The discharges with peak voltages between those of the major and minor types are so variable in voltage that it is hard to say whether they belong to one type or to several. But tentatively, we shall assume that they belong to a single type, which we shall call intermediate.

The types of discharge are also distinguished by the sequence in which discharges of the several types appear. The discharges occur commonly in trains of three or usually more members. The average interval between two discharges in a train is between .005 and .006 sec., as measured from the start of one to the start of the next. In the longer trains the interval is commonly less between the first members and greater between the last, being sometimes as short as .003 sec. at the beginning of the train and sometimes as great as .015 sec. at the end. For several reasons, the number and types of the discharges in one train are not always clear on the film.

The start or the end of a train is often lost in an unrecorded interval between two exposures. With both contacts near the head the minor discharge does not appear and with both contacts near the tail, the major and minor discharges are too much alike to be distinguished. However, a number of unambiguous traces were found on the film. Two of these are shown in Pl. I, Figs. 4 and 5. In Pl. I, Fig. 4, a minor discharge is followed by a number of majors, in this instance, five. This appears to be a characteristic combination of these two types, though the number of majors following the minor is found to vary from two to five, two being rare and more than five not being observed. (A sixth major could, however, be lost in an unrecorded interval between two exposures.) Pl. I, Fig. 5, shows a minor,



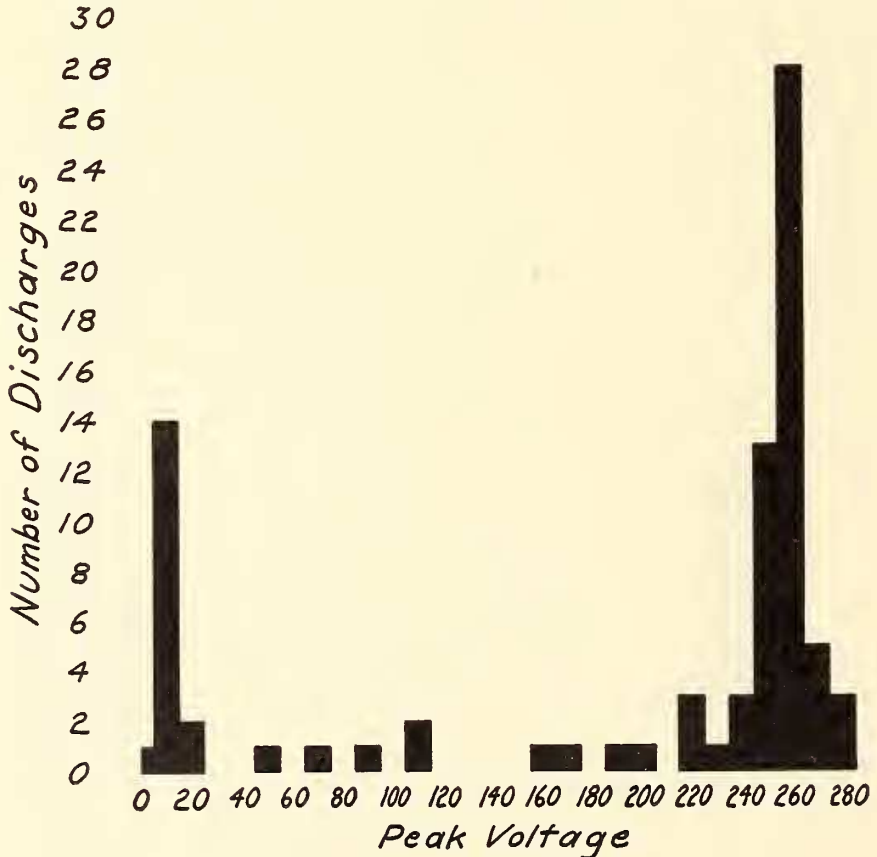
Text-figure 1.

Numbers of discharges with various peak voltages. Eel I. Contacts at snout and 85 cm. from snout.

quite small, followed by an intermediate and three majors. The marked difference in form between the intermediate and major discharges is to be noted. It is shown with a larger time scale in Pl. I, Fig. 11. It seems characteristic of the intermediate discharge that it occurs between a minor and a train of majors.

Certain apparent exceptions to these two kinds of train were recorded. There are two nearly certain instances of a single minor not followed by a major or an intermediate. Other examples of this have frequently been noticed visually. There is one instance, not quite certain, of a single major. There are a few cases in which the second discharge of a train, as well as the first, may be a minor, but it seems likely that it is an intermediate of low peak voltage. As against these instances there are some hundred and fifty cases in which a minor discharge is followed by a major or an intermediate discharge, the number of discharges afterward being sometimes determinable on the film and sometimes not.

Because of the quantity of film required for observations of this kind and the considerable labor involved in measuring so many peak voltages and time intervals, so extensive a series of discharges was recorded and studied only with Eel I. A fairly extensive series was recorded also with



Text-figure 2.

Numbers of discharges with various peak voltages. Eel I. Contacts at snout and 55 cm. from snout.

an eel 38 cm. long, and an inspection of the film showed some of the regularities just described.

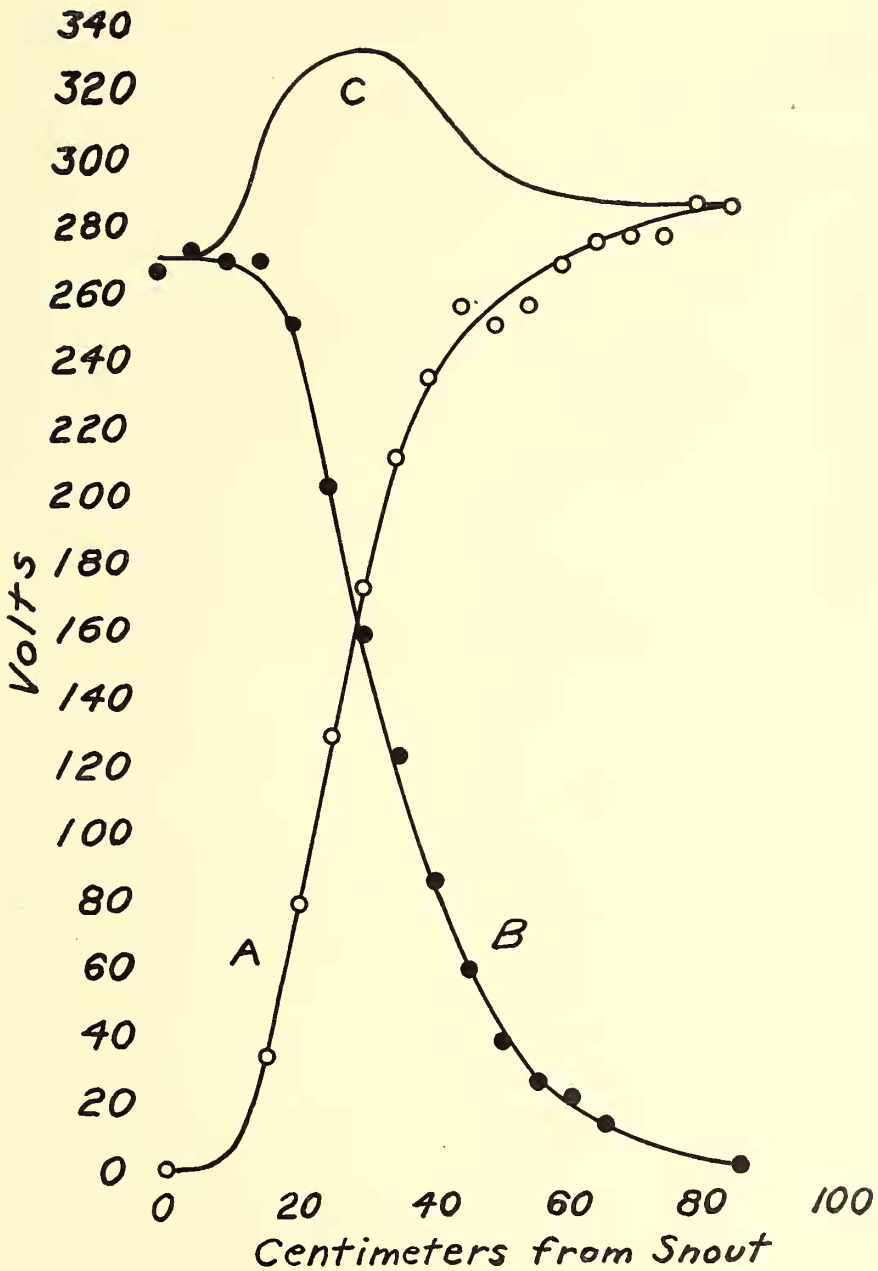
Tables I and II show the distribution with respect to peak voltage of all the discharges of Eel I measured in this way. In the observations recorded in Table I, one vertically deflecting plate was kept connected to the snout of the eel and the other was connected in turn to points 5 cm. along the eel. In the observations recorded in Table II, one contact was fixed 85 cm. from the snout while the position of the other was varied in steps.

From these tables, the mean peak voltage of the major discharge was found for each position of the contacts. The values are shown in Curves A and B of Text-fig. 3. For each curve the horizontal scale shows the distance of the variable contact from the snout. In curve A, plotted from Table I, the fixed contact is at the snout, and the peak voltage of the major discharge, shown on the vertical scale, increases as the variable contact is moved toward the tail. In curve B, plotted from Table II, the fixed contact is near the tip of the tail, 85 cm. from the snout, and the peak voltage de-

TABLE I.

Number of discharges with different peak voltages with one contact fixed at the snout end and the other at various distances from it along the body of the eel. Numbers of minor discharges are marked (*). Numbers of intermediate discharges are marked (#). All other numbers are of major discharges.

Peak Voltages from Snout to Variable Contact	Position of Variable Contact, Centimeters from Snout														
	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85
295-305													1	3	11
285-295													7	11	20
275-285						1	1		3	18	6	7	15	11	30
265-275						1	6	2	5	24	22	9	14	2	7
255-265						1	10	3	28	15	2	2	3		5
245-255						3	24	5	13	8	3	1			
235-245						10	1	1	3	2				1	
225-235					3	13	1		1						
215-225					3	7		1	3						
205-215					12			1							
195-205					5	2			1				1		
185-195					1				1#						
175-185				5	1							1#			
165-175				16					1#						
155-165				1					1#						
145-155															
135-145															
125-135				6											
115-125				2											
105-115									2#						
95-105															
85-95		1							1#						
75-85		14						1#							
65-75									1#						1#
55-65						1#									
45-55						1#			1#	1#	1#				
35-45	5	1, 1#								1#	1#		2*	2*	4*
25-35	10	1#	1#	1#	1#	1#	1#	1#		4*	2*, 1#	3*	4*	8*	10*
15-25	1#	1#	3#	3#	2*	7*	2*	1#	2*	14*	6*	3*	8*	8*	7*
5-15	1#	3#	3#	3#	2*	7*	7*	1*	14*	6*	2*		1	1	
0-5		2#		6*	7*	6*	1*	3*	1*						



Text-figure 3.

Mean peak voltages of major discharge between various points along eel. Eel I. A: One contact fixed at snout. B: One contact fixed at 85 cm. from snout. C: Sum of peak voltages of A and B.

originates in these organs, the more so as they are much the largest of the electric organs and most of the electric energy discharged by the eel is released in the major discharges.

The records in Tables I and II of the peak voltages of the minor discharge are not precise enough to enable curves to be drawn like those for the major discharge shown in Text-fig. 3. But from Table I it is clear that with one contact fixed at the snout the peak voltage of the minor discharge is very low until the variable contact is some 40 cm. from the snout. And from Table II it is clear that with one contact fixed at the tail the peak voltage is about the same for all positions of the variable contact nearer the snout than some 40 cm. At 60 cm. from the snout, the peak voltages of the major and minor discharges are about equal. It appears that the electromotive force of the minor discharge is generated in the posterior half of the eel, and most of it in the posterior third. This suggests that the minor discharge originates in the bundles of Sachs. These lie in the posterior half of the eel and, instead of having nearly their maximum cross-section at their anterior end, as the large electric organs have, they increase in cross-section for some distance toward the tail, finding room at the expense of the large organs, which taper off in the same region.

If the intermediate discharge has its special electric organ, as the major and minor discharges appear to have, then it probably originates in Hunter's organs. On the other hand, the fact that the intermediate discharge appears to take the place of a major discharge in the train of discharges, and the further fact that the major discharge next following an intermediate discharge is often of less than mean peak voltage indicate that the intermediate discharge is closely connected with the major discharge and suggest that it may be merely an anomalous form of the major discharge, instead of having a separate origin.

For the study of the variation of voltage in a single discharge, oscillographic traces on a much larger time scale than that of Pl. I, Figs. 4 and 5, are required. We have made a fairly thorough study only of the major discharge, as observed with Eels I and II. The timing period of the sweep circuit was set at 1/240 sec. The vertically deflecting plates of the oscillograph were connected to two points along the eel and the shutter of the camera was held open until the eel was provoked by gentle prodding to discharge. Particular attention was given to the potential differences developed in that part of the eel's length in which the large electric organs are of fairly uniform cross-section, in order to study the discharge without the complication caused by the tapering of the organs. In an eel of the size of these the large electric organs are of fairly uniform cross-section over a length of some 30 cm. starting almost at their anterior end. With each of these eels on open circuit, two series of oscillographic traces were recorded. In one series the fixed contact was 20 cm. from the snout and the variable contact was successively at positions equally spaced over a length of 30 cm. starting at the fixed contact. In the other series, the fixed contact was 50 cm. from the snout and the positions of the variable contact were the same as in the first series. Pl. I, Figs. 6-11, shows some of the traces so obtained with Eel I. Except in Pl. I, Fig. 11, which was reproduced because it shows an example of the intermediate discharge, all the traces shown are of major discharges. Time increases toward the right in all the pictures.

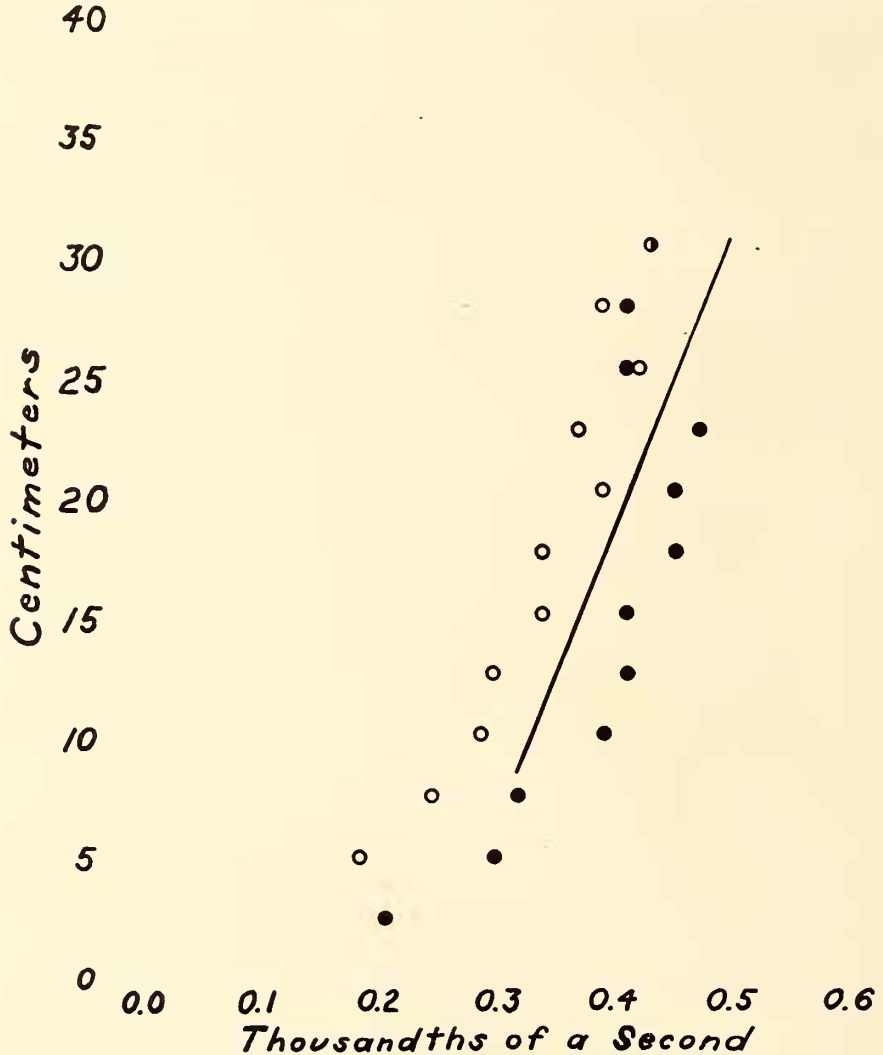
It will be seen at once that there is on each trace a sharp break between a period of rapidly rising voltage and a longer period of nearly steady voltage, and that there is a more gradual transition from the latter period to a period of falling voltage. Viewing the rising branch of the trace more closely, it is seen that the rate of increase of voltage, as measured by the slope of the curve, increases to a maximum at the place of steepest slope and, after holding this value briefly constant, falls quickly to zero at

the break of the curve. The description of a pulse of potential gradient given in the discussion of Plate I accounts, qualitatively at least, for these variations. It will be recalled that the pulse there described had a steep rising slope, a long plateau, and a fairly long falling slope. Consider a segment of the electric organ longer than the rising slope but shorter than the plateau. The segments with which the traces of Pl. I, Figs. 6-11, were obtained are probably all of such a length. As the pulse approaches the anterior end of the segment, the potential difference between the ends of the segment remains zero until the front of the rising slope enters the segment. Then the voltage starts to rise, at first slowly, however, not only because the part rendered active by the pulse is still short but also because the potential gradient near the front of the rising slope is still small. But as the rising slope advances into the segment, the rate of increase of voltage becomes greater, and when the whole rising slope is in the segment, the voltage is rising at maximum speed. This rate is maintained until the front of the rising slope passes the posterior end of the segment. The rate of increase of voltage in the segment then becomes less than the maximum, since some of the potential difference caused by the advance of the pulse is outside the segment. When the whole rising slope has passed out of the segment, leaving the segment entirely covered by the plateau, the potential difference over the segment is constant, since the potential gradient is constant at every point. Then, as the front of the falling slope enters the segment, the voltage begins to fall, but slowly at first, because the region of falling potential gradient is still short. As the pulse advances farther the rate of fall increases. The fall is probably near its steepest when the front of the falling slope reaches the posterior end of the segment and the potential gradient is no longer sustained in any part.

As the pulse of potential gradient runs down the electric organ, all points ahead of the pulse are at the same potential. Consequently, when the front of the pulse has passed the first of a set of points along the organ, but has not yet reached the second, the potential difference between the first and second is the same as between the first and third, and so on. Hence, in a series of traces obtained with a fixed anterior contact and a variable posterior contact, the rising branches of the various traces should all be identical almost to the break. Or, more strictly, since successive discharges do not give exactly the same trace even with both contacts the same, what we should expect is that the traces obtained with different positions of the posterior contact should show no greater differences up to the break than do traces obtained with the same position of the posterior contact. In our observations this appears to be true. If then in such a series of traces the mean time intervals from the start of the discharge to the break be measured for two positions of the variable contact, the difference in these intervals should be the time the pulse takes to travel from one position to the other. Such measurements were made on a large number of traces in the series illustrated by Pl. I, Figs. 6-11. The results are shown by the solid circles of Text-fig. 4, the distances between the fixed and variable contacts being plotted vertically and the time intervals horizontally. The open circles show the corresponding distances and time intervals as measured on the traces obtained with a fixed posterior and a movable anterior contact. The argument in this case is like that in the other except that in this case the break would occur at the same instant for all positions of the anterior electrode, while the start of the discharge would occur earlier the farther the anterior contact was from the posterior.

Even with care only very crude measurements are possible, and the information obtained about the speed of the pulse is only qualitative. A smooth curve drawn to fit as well as possible either the solid or the open circles will have a slope increasing toward the right, and from this it may at first appear that the pulse runs down the electric organ with an ac-

celerated motion. This interpretation is, however, not justified, for the lower solid circles refer to the region just more than 20 cm. from the snout, while the lower open circles refer to the region just less than 50 cm. from the snout, and vice versa for the upper circles. It seems likely that the points below 10 cm. on the vertical scale should be ignored in reckoning the speed of the pulse, since the rising slope of the pulse may itself be somewhere near 10 cm. long. The other points are spread along a roughly indicated slope. The line drawn in the figure has a slope corresponding to a speed of 1,200 meters per second, but this should not be taken as giving



Text-figure 4.

Distances traversed by the potential pulse of major discharge in various intervals of time. Eel I. Black circles: Fixed contact at 20 cm. from snout. Movable contact at distances toward tail from fixed contact as shown on vertical scale. White circles: Fixed contact at 50 cm. from snout. Movable contact at distances toward snout from fixed contact as shown on vertical scale.

more than the general order of magnitude of the speed of the pulse in Eel I.

Pl. II, Figs. 1-5, shows traces obtained with Eel II corresponding to those for Eel I shown in Pl. I, Figs. 6-11. The general character of the discharge appears similar in the two eels, but neither the break in the rising branch nor the flat top of the trace is marked with Eel II as with Eel I. (These features are less marked also with any of the smaller eels we have studied. In the visual observations reported in our previous paper, we did not notice them at all.) Because the break is not so sharp with Eel II as with Eel I, and also because the number of traces photographed is smaller, a figure like Text-fig. 4 made from the traces obtained with Eel II tells even less than Text-fig. 4. The data suggest for the major discharge of Eel II a speed of the general order of 800 meters per second, to be compared with the estimate of 500 meters per second made for the same eel from Pl. I, Figs. 1-3.

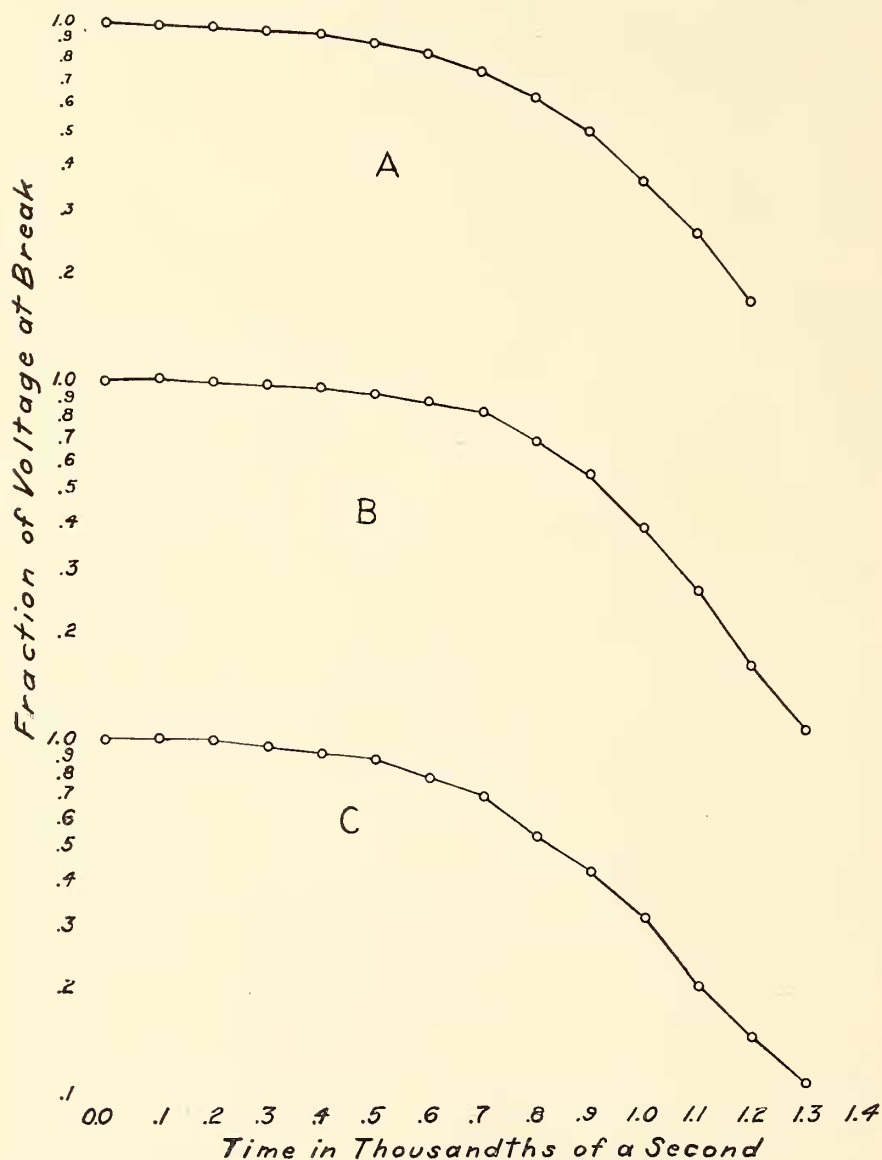
From the break on, different traces obtained with the same eel do not differ greatly except in the vertical scale. This is shown in Text-fig. 5, in which the ratio of the voltage at any instant to the peak voltage is plotted vertically and the time after the break is plotted horizontally from measurements on the traces of three discharges of Eel II. The vertical scale is logarithmic; that is, equal distances represent equal intervals in ratio. Each of the three curves shown ends on the right in an approximately straight falling branch. The scale of voltage being logarithmic, this indicates that the fractional rate of decrease of the voltage is constant; that is, the time required for the voltage to drop by one-half, for example, is the same whether the voltage be high or low. This type of decrease is characteristic of the voltage of an electric capacity discharging through a resistance, and it may be that some such mechanism is operative in the electric organs.

The time interval between the instant at which the rising branch of the trace breaks and the instant at which the fractional rate of decrease becomes constant is very closely the same for one eel whatever the distance between the contacts. The rising branch breaks when the front of the plateau of the pulse reaches the posterior contact. It seems likely that the fractional rate of decrease of potential gradient becomes constant at any one point when the rear end of the plateau passes that point, and consequently the fractional rate of decrease of potential difference between two contacts becomes constant when the rear end of the plateau passes the posterior contact. If this is true, the interval noted is the time taken for the entire plateau of the pulse to pass a given point on the electric organ. From Text-fig. 5 this interval is about .001 sec. for Eel II. The length of the plateau was reckoned at about 50 cm. in the discussion of Pl. I, Figs. 1-3, and the speed of the pulse would thus be 500 meters per second. This is the same as the first estimate made for this eel.

It may be worth while to remark that the plateau of the pulse not only prolongs the discharge but also increases the peak voltage developed over the whole electric organ. High voltages over the whole organ are developed only by the addition of the voltages in different segments, and the highest voltage that can be developed in the whole organ is only the voltage that can be developed in whatever length of the organ is active at one time. If the length of the organ were increased without an increase in the length of the plateau, the discharge would last longer without attaining a much higher peak voltage, and if the length of the plateau were decreased without a change in the length of the organ, the discharge would last as long as before but would not attain so high a peak voltage.

In order to get some notion of the power of the discharge, a variable resistance was connected between points at 20 and 70 cm. from the snout of Eel I, and the vertically deflecting plates of the oscillograph were con-

nected to measure the voltage developed across this resistance. From the values of the voltage and the resistance, the power externally delivered in the discharge could be calculated. The circles in Text-fig. 6 show the power at the peak of the discharge found with different observed values of the

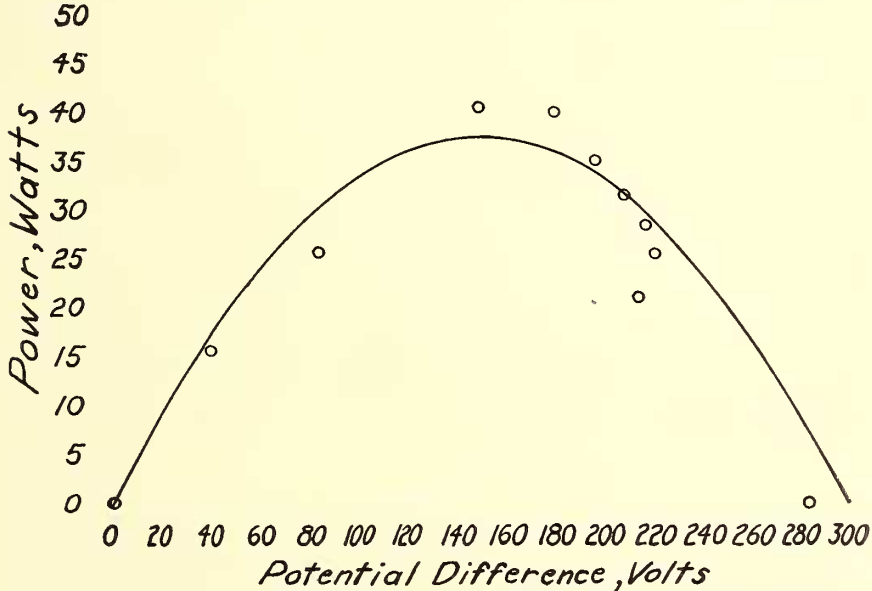


Text-figure 5.

Decay of potential difference in major discharge. Eel II. Horizontal scale shows time measured from break in potential difference. Vertical scale shows potential difference plotted logarithmically, potential difference at break being taken as unity. A: Contacts at 20 and 40 cm. from snout. B: Contacts at 30 and 50 cm. from snout. C: Contacts at 20 and 50 cm. from snout.

voltage. The maximum external power is about 40 watts and is found at a voltage about half the open-circuit voltage. Since an electromotive force operating through a fixed internal and a variable external resistance also delivers maximum power externally at half the open-circuit voltage, there has been drawn for comparison with the observations the power-voltage curve for an electromotive force of 300 volts and an internal resistance of 600 ohms. The same eel in a tank filled with the water to which it is accustomed develops between the same points of contact a potential difference of 150 volts. The water, being in contact with the whole skin of the eel, is of course not electrically equivalent to a resistance connected between two points. Neither is there any reason to expect that the electric organ can be represented even approximately by an electromotive force and an internal resistance.

Nevertheless, although the argument can not be made at all precise, it seems likely that the evolution of the eel has brought about such a series-parallel connection of the electromotive elements as to approach the condition for maximum external power. In this connection, a comparison of the different species of electric fishes is suggestive. The fresh-water species, the Electric Eel, the Electric Mormyridae, and the Electric Catfish, all have longitudinal electric polarity. The first two are long in proportion to their width and thus well adapted in shape to the development of a prevailingly series connection to build up a high electromotive force against the high external resistance of fresh water. The electric organ of the Electric Catfish forms a sheath under its skin and is also of small cross-section in comparison with its length. Both the Electric Ray and the Star-gazer, on the other hand, have a polarity between their upper and lower surfaces and their shape is suited with this polarity to a prevailingly parallel connection for a low internal resistance against the low resistance of the salt water in which they live. Those members of the ostracoderms, fossil fish-like



Text-figure 6.

Peak potential difference and power developed by major discharge in various resistances connected between points 20 and 70 cm. from snout. Eel I.

chordates, which Stensiö believes to be electric and which were supposedly marine in habitat, also seem to have had a polarity between the upper and lower surfaces.²

The maximum energy delivered externally in one discharge was computed from the same traces as were used to find the power. It was found to be between .03 and .04 joule. More than a hundred discharges would be required to deliver externally one gram-calorie. The energy of a discharge under water is doubtless different from this but is probably of the same order of magnitude.

The average electric power which the electric organ can continue to deliver over any considerable length of time does not appear to be greater than the mechanical power developed by a muscle of the same size. The speed with which peak power is attained is doubtless much greater in electric than in muscular tissue. The electric discharge has, it seems, no retarding factor comparable to mechanical inertia in muscular activity.

The rate at which the power attains its peak value is determined in part by the speed with which the pulse of potential gradient runs down the electric organ. This speed, according to our estimates, (from 500-1,000 meters per second), is so much higher than the reported speeds of propagation of nerve impulses as to raise some doubt whether or not the discharge is propagated or only initiated by a nervous impulse. There is another observation which appears hard to reconcile with the supposition of a nervous propagation. Impulses along nerves commonly show dispersion; the impulse is divided among a number of parallel nerve fibres along which it travels at different speeds. Thus the impulse spreads as its swifter components draw away from the slower. Nothing of this sort is observed in the propagation of the discharge of the electric eel. The break in the rising branch of the oscillographic trace is just as sharp at some distance down the electric organ as it is at the anterior end, and the interval from the break to the start of uniform fractional decrease is no longer in a posterior than in an anterior segment. Although these considerations are probably not final against the hypothesis of nervous propagation, they at least suggest that an alternative hypothesis should be sought.

In the discharge of the electric organ a very large number of cellular electromotive forces must act in series. It can hardly be that the cells are permanently connected in series and are kept steadily charged, for the tissue of the eel can not be expected to provide insulation against such a voltage. It may be that they are permanently connected in series but their electromotive forces are generated only at the commencement of the discharge. Or it may be that they are fully charged in the inactive state of the organ but are connected in series only during the discharge. On the latter assumption, which at present seems preferable, the charging process might be an electrochemical process of the same kind as occurs in ordinary tissue. The connection in series might be made by a breakdown in insulation between cells. If this be true, the action of the electric tissue would resemble that of the impulse generator recently developed for the production of high voltage. But any such speculation as this requires testing by further experiments.

SUMMARY.

Voltages and speeds of propagation of the electrical impulse along the body of the Electric Eel have been measured. These indicate that an anterior point on the body of the eel is always positive to a posterior point.

²The work of Sanderson and others on *Raia clavata*, etc., does not seem to fit into this theory. They report a spindle-shaped organ, weakly electric, situated in the tail. Since the order of voltage reported, (0.5 volts per centimeter of length), is what might be expected, according to the hypothesis, in a marine animal, we are willing to advance it as a basis for further, more conclusive, investigations of the discharges of the Skates.

Peak voltages of the order of 300 and peak wattage of the order of 40 are indicated as maximum for eels exceeding 50 cm. long.

The velocity of the pulse along the body of the eel is between 500 and 1,000 meters per second.

Two types of discharge are definitely identified and a third tentatively identified.

The electrical discharges commonly occur in trains of one minor member followed by from three to six major members separated in time by an average of .005 seconds.

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Note: Additional references, particularly to the torpedo, may be found in Dean. 1916-1923, vol. III [Index volume] under Electrical Fishes (pp. 406-408).

EXPLANATION OF THE PLATES.

PLATE I.

- Fig. 1. Phase difference of discharge in anterior and posterior segments. Eel II. Horizontal deflection caused by segment from 15 to 35 cm. from snout. Vertical deflection caused by segment from 35 to 70 cm. from snout.
- Fig. 2. Same connections as in Fig. 1.
- Fig. 3. Sense of propagation of pulse. Eel II. Horizontal deflection of timing circuit, period $1/60$ sec., time increasing to right. Vertical deflection downward by segment from 20 to 25 cm. from snout. Vertical deflection upward by segment from 50 to 70 cm. from snout.
- Fig. 4. Train of 1 minor and 5 major discharges. Eel I. Timing period $1/20$ sec.
- Fig. 5. Train of 1 minor, 1 intermediate, and 3 major discharges. Eel I. Timing period $1/20$ sec.

Major discharges. Eel I. Timing period $1/240$ sec.

- Fig. 6. Contacts at 20 and 30 cm.
- Fig. 7. Contacts at 20 and 40 cm.
- Fig. 8. Contacts at 20 and 50 cm.
- Fig. 9. Contacts at 30 and 50 cm.
- Fig. 10. Contacts at 40 and 50 cm.
- Fig. 11. Intermediate discharge shown at center of trace. Note initial spur and round top.

PLATE II.

Major discharges. Eel II.

Figs. 1-5. Contacts and timing period same as in Pl. I, Figs. 6-10.

Major discharges under various loads. Eel I. Contacts at 20 and 70 cm. from snout. Timing period $1/240$ sec.

- Fig. 6. Open circuit.
- Fig. 7. 1,950 ohms.
- Fig. 8. 820 ohms.
- Fig. 9. 280 ohms.